NeoBiota 19: 45–65 (2013)
doi: 10.3897/neobiota.19.5279
www.pensoft.net/journals/neobiota

REVIEW ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

The ecology, biogeography, history and future of two globally important weeds: *Cardiospermum halicacabum* Linn. and *C. grandiflorum* Sw.

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Academic editor: *J. Kollmann* | Received 8 April 2013 | Accepted 9 July 2013 | Published 11 October 2013

Citation: Gildenhuys E, Ellis AG, Carroll SP, Le Roux JJ (2013) The ecology, biogeography, history and future of two globally important weeds: *Cardiospermum halicacabum* Linn. and *C. grandiflorum* Sw. NeoBiota 19: 45–65. doi: 10.3897/neobiota.19.5279

Abstract

Members of the balloon vine genus, *Cardiospermum*, have been extensively moved around the globe as medicinal and horticultural species, two of which are now widespread invasive species; *C. grandiflorum* and *C. halicacabum*. A third species, *C. corindum*, may also have significant invasion potential. However, in some regions the native status of these species is not clear, hampering management. For example, in South Africa it is unknown whether *C. halicacabum* and *C. corindum* are native, and this is a major constraint to on-going biological control programmes against invasive *C. grandiflorum*. We review the geography, biology and ecology of selected members of the genus with an emphasis on the two most widespread invaders, *C. halicacabum* and *C. grandiflorum*. Specifically, we use molecular data to reconstruct a phylogeny of the group in order to shed light on the native ranges of *C. halicacabum* and *C. corindum* in southern Africa. Phylogenetic analyses indicate that southern African accessions of these species are closely related to South American taxa indicating human-mediated introduction and/or natural long distance dispersal. Then, on a global scale we use species distribution modelling to predict potential suitable climate regions where these species are currently absent. Native range data were used to test the accuracy with which bioclimatic modelling can identify the known invasive ranges of these species. Results show that *Cardiospermum* species have potential to spread further in already invaded or introduced regions in Australia, Africa and Asia, underlining the importance of resolving taxonomic uncertainties for future management efforts. Bioclimatic modelling predicts Australia to have highly favourable environmental conditions for *C. corindum* and therefore vigilance against this species should be high. Species distribution

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modelling showed that native range data over fit predicted suitable ranges, and that factors other than climate influence establishment potential. This review opens the door to better understand the global biogeography of the genus *Cardiospermum*, with direct implications for management, while also highlighting gaps in current research.

Keywords
Balloon vines, biological invasion, *C. corindum*, management, phylogeny, species distribution modelling

Rationale

Understanding the biology, ecological requirements, and native distributions of potentially invasive species is crucial to ensure effective management and to predict their potential invasiveness. We review these attributes for selected members of a globally weedy genus, *Cardiospermum*, commonly known as balloon vines. We review the ecology and history of anthropogenic range expansion of the genus, with special emphasis on the two most problematic species in the group, *C. grandiflorum* and *C. halicacabum*. On a regional scale we aim to resolve the native provenance(s) of balloon vine species found in southern Africa, using a phylogenetic approach. Lastly, on a broad scale we assess the invasion risk posed by balloon vine species found outside their supposed native ranges, using species distribution modelling. Moreover, to evaluate the merit of this commonly employed method, we compare data of known invaded areas to predictions based on native range records.

Biogeography and phylogeny of selected *Cardiospermum* taxa

The genus *Cardiospermum* L. 1753 (family Sapindaceae, tribe Paullinieae) currently consists of 17 shrub, subshrub, climber, and erect species, commonly called balloon vines (Subramanyam et al. 2007). Around half of the species occur in moist tropical and subtropical regions while others are arid-adapted (Ferrucci and Urdampilleta 2011). Thirteen *Cardiospermum* species (*C. oliveirae*, *C. urvilleoides*, *C. procumbens*, *C. pterocarpum*, *C. anomalum*, *C. pygmaeum*, *C. cristobaliae*, *C. tortuosum*, *C. bahianum*, *C. integerrimum*, *C. heringeri*, *C. cuchujaquense*, *C. dissectum*) are mostly restricted in and around the Neotropics from south-eastern Brazil to north-central Mexico (Ferrucci and Umdiriri 2011) with most found in Brazil (12 spp.). Nine species are restricted to Brazil while the remaining eight species display wider geographical distributions. *Cardiospermum pterocarpum* occurs in Brazil, Argentina and Paraguay. *Cardiospermum pygmaeum, C. dissectum* and C. *cuchujaquense* are restricted to Mexico with *C. dissectum* also having been recorded in Texas, USA. *Cardiospermum pechuelii* is the only taxon restricted to Africa, occurring only in the desert areas of Namibia. Three species, *C. corindum*, *C. halicacabum* and *C. grandiflorum* have near cosmopolitan distributions (Ferrucci and Umdiriri 2011, Urdampilleta et al. 2012).

Morphology divides this genus into three sections; *Cardiospermum* Radlk., *Carphospermum* Radlk. and *Ceratadenia* Radlk. (Urdampilleta et al. 2012). In addition to *Cardiospermum*, Paullinieae includes five other genera, *Serjania*, *Paullinia*, *Urvillea*, *Houssayanthus* and *Lophostigma*, of which *Urvillea* is regarded the sister genus to *Cardiospermum* (Ferrucci and Acevedo-Rodrigues 1998).

Only four *Cardiospermum* species occur abundantly outside the neotropics: *C. halicacabum*, *C. grandiflorum*, *C. corindum*, and *C. pechuelii* (Burke 2003, Ferrucci and Umdiriri 2011). *Cardiospermum pechuelii* may be the only true African taxon, found in the Namib Desert (Burke 2003, Simelane et al. 2011). *Cardiospermum pechuelii* is morphologically similar to other arid adapted species, such as *C. dissectum* from Mexico. The most widely distributed species are tropical and subtropical *Cardiospermum corindum* (Fig. 1A), *C. grandiflorum* (Fig. 1B) and *C. halicacabum* (Fig. 1C) (Mc Kay et al. 2010, Simelane et al. 2011). All three species occur in the Neotropics and subtropical southern Africa. *Cardiospermum corindum* is also found in parts of India where it is known under its synonym name *C. canescens* (The Plant List 2010, Raju et al. 2011). *Cardiospermum grandiflorum* and *C. halicacabum* are present in Australia and other Pacific islands classified as alien or invasive, and *C. halicacabum* is also present in Europe and Asia (Subramanyam et al. 2007). In many of these countries the native status of these species is highly debated and their biogeographical history remains uncertain (Table 1). *Cardiospermum grandiflorum*, *C. corindum* and *C. halicacabum* are regarded as being native in South and Central America while the status of *C. halicacabum* is questioned in North America (Henry and Scott 1981, Bowen et al. 2002, Carroll 2007, Goosem 2008) and tropical Africa (USDA, United States Department of Agriculture; Weeds of Australia). Similarly the status of *C. corindum* is uncertain throughout the African continent (Henderson 2001, Simelane et al. 2011). In Asia *C. halicacabum* is variously regarded as either alien or native (Venkatesh and Krishnakumari 2006, Subramanyam et al. 2007).

Invasion history of the genus *Cardiospermum*

Alien invasive species are a global concern and a threat to biodiversity (Pimentel et al. 2000, Van Wilgen et al. 2001). They also negatively impact agricultural and forestry sectors with substantial economic costs associated with their direct impacts, eradication, control and restoration efforts (Pimentel et al. 2000, 2001). Like many invasive species, *Cardiospermum* species have been introduced for their economic value prior to becoming problematic (Pimentel et al. 2000, Van Wilgen et al. 2001). *Cardiospermum* species have been extensively moved around the world for both their medicinal (Venkatesh Babu and Krishnakumari 2006, Subramanyam et al. 2007) and ornamental (Carroll et al. 2005a) values.

The ornamental attraction of *Cardiospermum* species are their inflated balloon shaped fruit (Fig. 2). Coincidently this trait also contributes to their colonisation success, since these balloons can float in seawater and stay viable for long periods of time, facilitating long distance dispersal, even between landmasses (Carroll et al. 2005a, Simelane et al. 2011). For example, *C. grandiflorum* was introduced to the Cook Islands as a result of a

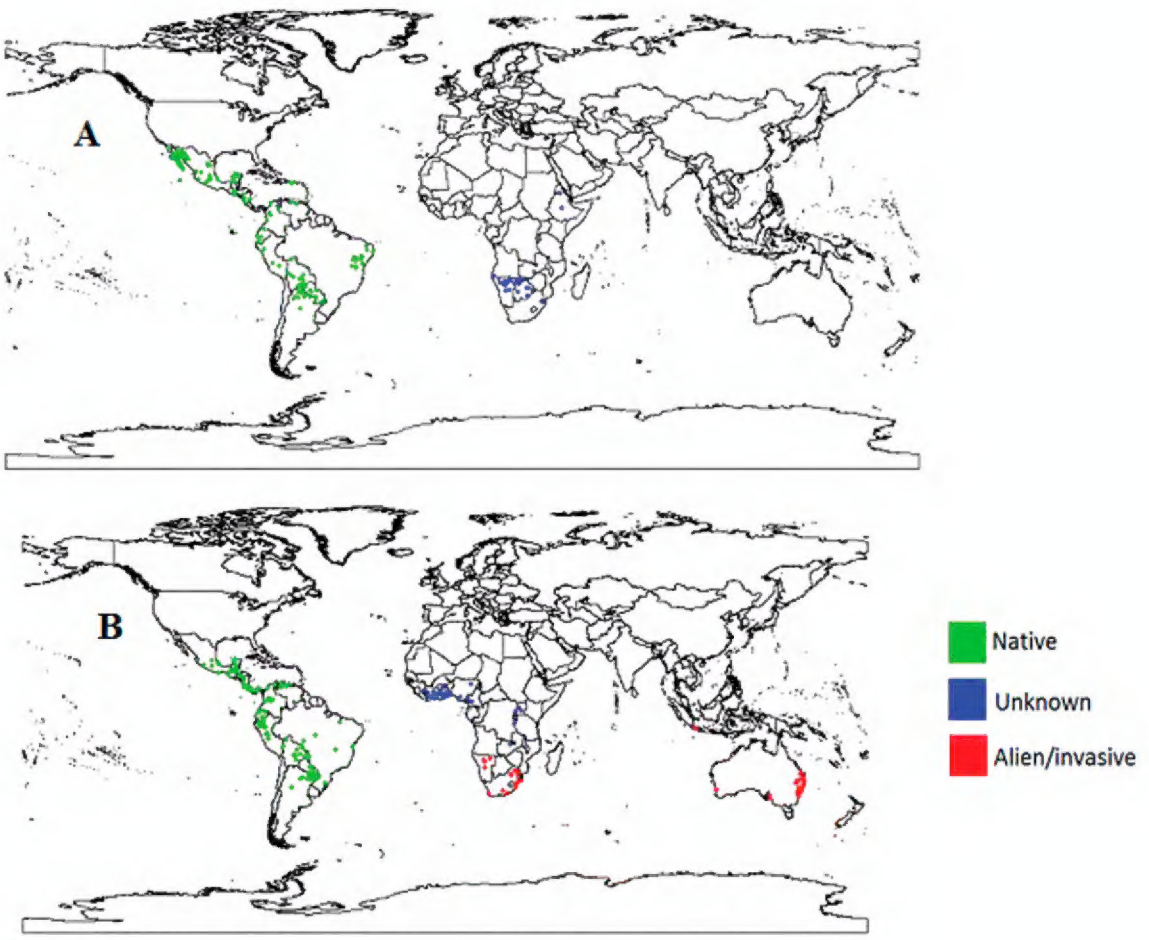

Figure 1. Distribution of *Cardiospermum* species. Global distribution of **A** *C. corindum* **B** *C. grandiflorum* and **C** *C. halicacabum* in native, unknown and alien or invasive regions.

hurricane (Meyer 2004), whilst increased spread of balloon vines in Australia was associated with a major cyclone and subsequent flooding (Carroll et al. 2005a). We floated *C. grandiflorum* fruit structures in seawater and found some of them capable of floating more than 25 weeks with seed remaining viable. (E. Gildenhuys et al., unpubl. data). Upon dehiscence, each seed is attached to a circular blade that permits further transport by wind.

Invasive *Cardiospermum* species are considered "transformer weeds" (Mc Kay et al. 2010), as they often extensively cover native vegetation, depriving it of sunlight and thus photosynthesis (Mc Kay et al. 2010, Simelane et al. 2011). *Cardiospermum* invasions also have substantial economic impacts on sugarcane and soybean production (Johnston et al. 1979, Jolley et al. 1983, Voll et al. 2004, Subramanyam et al. 2007, Murty and Venkaiah 2011). For example, in Brazil *C. halicacabum* reduces soybean crop yields by

Table 1. Details of uncertain native or non-native statuses of two *Cardiospermum* species in North America and Africa.

	Continent	References for debated native/non-native status
C. halicacabum	North America	Brizicky 1963, James 1825, Carroll and Boyd 1992
	Africa	Brizicky 1963, Davies and Verdcourt 1998, Hyde et al. 2012a, Hyde et al. 2012b, Henderson 2001, Foxcroft et al. 2008, Simelane et al. 2011
C. corindum	Africa	Davies and Verdcourt 1998, Henderson 2001, Simelane et al. 2011, Germishuizen et al. 2006, Adeyemi and Ogundipe 2012
	North America	Brizicky 1963, Castellanos et al. 1999, Molina-Freaner and Tinoco-Ojanguren 1997

up to 26% (Dempsey et al. 2011, Brighenti et al. 2003). The problem with controlling *Cardiospermum* infestations in soybean crops is the difficulty of mechanically excluding their seeds, which are similar in size and shape to those of soy (Brighenti et al. 2003).

Two balloon vine species well-travelled

Currently two *Cardiospermum* species are globally considered important invaders. *Cardiospermum grandiflorum* is classified as an invasive species in Australia, southern Africa, Cook Islands and many other Pacific islands (Mc Kay et al. 2010) while *C. halicacabum* is considered a weed in Australia with its status (native or introduced) undetermined in most other parts of its range (Henderson 2001, Harris et al. 2007). In Australia, *C. grandiflorum* is considered amongst the "most destructive life forms of rainforests" (Werren 2002), while in South Africa *C. grandiflorum* is classified as a Category 1 weed which means it's cultivation is prohibited and control is mandatory (Henderson 2001).

South Africa's Working for Water program launched a research initiative in 2003 to find biological control agents against *C. grandiflorum* (Simelane et al. 2011). Eight insects and two fungal agents have been identified and are currently undergoing host-specificity testing in South Africa (Simelane et al. 2011). Most are capable of feeding and developing on other *Cardiospermum* spp. in South Africa, in particular *C. halicacabum* and *C. corindum* (Mc Kay et al. 2010). Three promising agents were identified, a seed-feeding weevil (Curculionidae: *Cissoanthonomus tuberculipennis*), a fruit-galling midge (Cecidomyiidae: *Contarinia* spp.) and the rust fungus *Puccinia arechavaletae* (Simelane et al. 2011). Concerns about potential non-target impacts of candidate control agents on *C. corindum* and *C. halicacabum,* as well as the debated native status of these congeners in southern Africa (Table 1), have so far prevented the release of these agents.

Invasion histories of *C. grandiflorum* and *C. halicacabum*

The ornamental trade of *Cardiospermum halicacabum* and *C. grandiflorum* spans more than 100 years. For example, in Australia the first herbarium records of *C.*

grandiflorum date back to 1923, collected around Sydney, New South Wales (Carroll et al. 2005a). Currently invasive populations are found throughout the east coast of Australia between Sydney and Cairns although less abundantly to the north of Brisbane (E. Gildenhuys, pers. obs.). More recently the species has spread inland to forest areas such as Toowoomba (Queensland) and the Blue Mountains (New South Wales) (Carroll et al. 2005a, E. Gildenhuys, pers. obs.). *Cardiospermum halicacabum* is more abundant in the northern parts of Australia such as Darwin and Cairns, and is seldom found along the east coast south of Rockhampton, Queensland (E. Gildenhuys, pers. obs.). It is speculated that *C. halicacabum* was introduced during James Cook's second voyage in the 1770's long before the introduction of *C. grandiflorum* (Bean 2007, Harris et al. 2007).

The introduction of *Cardiospermum grandiflorum* into South Africa occurred approximately 100 years ago (Simelane et al. 2011). Today it is classified as a major weed, and is present and considered invasive in five provinces, of which Kwazulu-Natal and the Eastern Cape are the most affected (Henderson 2001, Simelane et al. 2011). The first records of *C. halicacabum* in South Africa dates back to 1917, 1919 in Namibia and 1930 in Botswana (Global Biodiversity Information Facility: GBIF, http://data.gbif.org/welcome.htm). It is classified as a minor weed in southern Africa, though its native status is debated, with slight impacts compared to *C. grandiflorum* (Henderson 2001).

Cardiospermum halicacabum and *C. grandiflorum* are also present in North America (Carroll and Loye 2012). *Cardiospermum halicacabum* is more widespread than *C. grandiflorum*, the latter apparently restricted to a small area in suburban Los Angeles (S. Carroll, pers. obs.). Due to the evident ability of some *Cardiospermum* species to disperse over long distances (Carroll et al. 2005a, Simelane et al. 2011), it is possible that the presence of *C. halicacabum* in North America is due to natural dispersal from South and Central America, rendering a native status. On the other hand, if seeds escaped horticultural and agricultural environments, they should be awarded non-native status (Subramanyam et al. 2007). *Cardiospermum halicacabum* was reported in the Spontaneous Illinois Vascular Flora before 1922 and was described as abundant in Oklahoma in the 1820's (James 1825); thus, if not native, *C. halicacabum* was introduced more than 180 years ago.

Cardiospermum halicacabum is also present in China and India. In China it is described as a common weed in forest margins, shrublands, grasslands, cultivated areas and wastelands of the east, south and southwest (Flora of China, www.eFloras.org) – though considered native by some – [Pacific Island Ecosystems at Risk (PIER)]. In India it is widespread and considered non-native (Raju et al. 2011). The history of *C. halicacabum* in these countries is unknown, but it is widely used for medicinal purposes (Subramanyam et al. 2007).

Biology and ecology of *C. grandiflorum* and *C. halicacabum*

A comprehensive understanding of the biology and ecology of *C. halicacabum* and *C. grandiflorum* is important because of the invasive potential and biogeographic uncer-

tainties which characterise these two taxa. Such information will also contribute to making informed decisions on their conservation (if native) or control (if invasive). This is especially true since the extent to which these species are invasive is essentially unknown and the uncertainties of their classification in most areas suggest the possibility of a cosmopolitan native distribution.

The morphology of these two species is similar, with both being adapted for tropical and subtropical climates. *Cardiospermum grandiflorum* is a large, semi-woody perennial, whereas *C. halicacabum* is smaller, less woody and commonly annual. *Cardiospermum grandiflorum* has elongated fruit (4.5–6.5 cm in length) compared to the more compact fruit of *C. halicacabum* (2.5–3.0 cm in length) (Fig 2A and B). Fruit structures consist of three dorsally keeled membranous capsules each consisting of three internal blades (Weckerle and Rutishauser 2005). The fruit are septifragal with the capsules breaking away from each other when fruit are ripe, changing colour from green to brown (Weckerle and Rutishauser 2005). Seeds of the two species differ, with a kidney shaped hilum on *C. halicacabum* seeds and a round hilum on *C. grandiflorum* seeds. Both species normally produce three seeds per fruit (Weckerle and Rutishauser 2005), are climbers with tendrils and have large flat biternate leaves. The leaves and stems of *C. grandiflorum* have small reddish hairs that are absent in *C. halicacabum* (Henderson 2001). Flowers are white and yellow with *C. halicacabum* flowers smaller (2–3 mm) compared to those of *C. grandiflorum* (7–11 mm) (Henderson 2001). The average length of *C. halicacabum* is 1–3 m, while *C. grandiflorum* is slightly taller with an average of 2–5 m, though both are capable of greatly exceeding these lengths (Henderson 2001).

Both taxa produce flavone aglycones and cyanogenic compounds that likely protect them against predators such as soapberry bugs (Subramanyam et al. 2007). Soapberry bugs (genera *Leptocoris, Jadera* and *Boisea* from the family Rhopalidae) feed exclusively on seeds of Sapindaceae and are predators of *Cardiospermum* (Carroll et al. 2005b, Carroll 2007). An example of the impact of invasive *Cardiospermum* populations includes an evolved increase in beak length of the native *Leptocoris tagalicus* soapberry bug feeding on invasive *C. grandiflorum* in Australia (Carroll et al. 2005b). Soapberry bugs co-occur with the widespread distribution of *Cardiospermum* and thus may be a factor in *Cardiospermum* reproduction globally. A treatment of soapberry bugs that feed on *C. halicacabum* and *C. grandiflorum* can be found in Carroll and Loye (2012).

The germination and growth success of *Cardiospermum halicacabum* is well studied because of its medicinal value, as well as its impact on soybean plantations and on natural riparian areas (Dempsey 2011). In contrast, no studies exist addressing these topics for *C. grandiflorum,* despite the need for additional biological information about this environmental weed. Optimum germination of *C. halicacabum* takes place at 35°C, with high oxygen concentrations increasing germination success (Johnston et al. 1979, Jolley et al. 1983, Dempsey 2011). Therefore, in natural habitats, establishment may be more likely in conditions with warm, well-oxygenated soils. Seeds and young plants are able to survive flooded, saturated and dry conditions while performing best in intermediate conditions (Dempsey 2011).

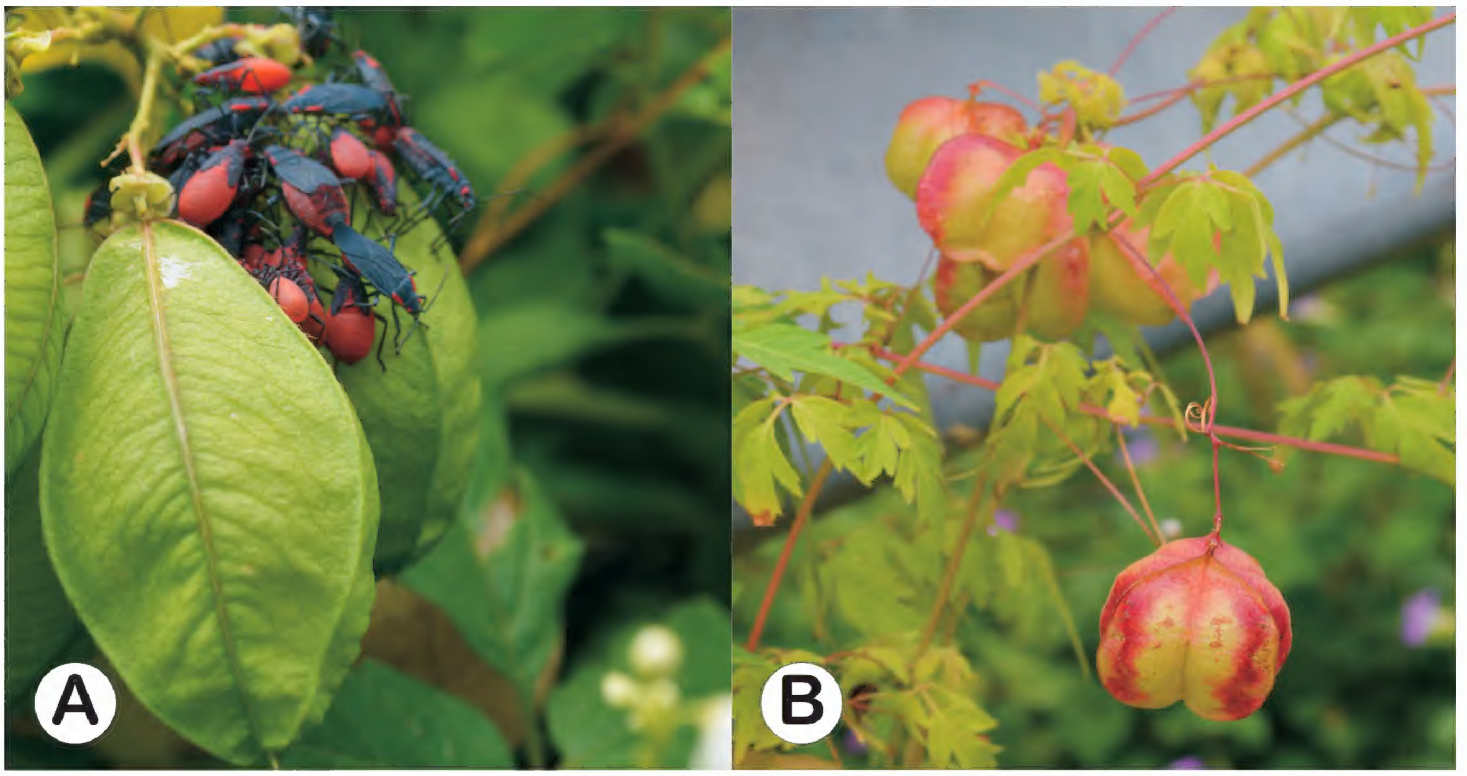

Figure 2. *Cardiospermum* fruit. The ornamental attraction of *Cardiospermum* plants and the reason for their widespread distribution is their balloon shaped fruit **A** *C. grandiflorum* (JJ Le Roux) and **B** *C. halicacabum* (JJ Le Roux).

Despite morphological similarity, these two species differ markedly. They occasionally occur sympatrically but mostly prefer different habitats with *C. halicacabum* dominating tropical and *C. grandiflorum* subtropical areas (Henderson 2001). Although both species invade forest margins and watercourses, *C. grandiflorum* also thrives in disturbed urban open areas while *C. halicacabum* predominantly invades wood- and grasslands which highlights its threat to plantations (Henderson 2001).

Management of invasive *Cardiospermum*

To date, managing and reducing impacts of *Cardiospermum* invasions has mostly involved manual removal or burning (Subramanyam et al. 2007). Manual removal involves cutting plants at the base enabling the top part to die off after which roots are dug out which is thus labour intensive (Mc Kay et al. 2010). Chemical control of larger plants includes treatment with paraquat, glufosinate-ammonium, lactofen, carfentrazone-ethyl, sulfentrazone, glyphosate or 2, 4-dichloraphenoxy acetic acid (Subramanyam et al. 2007). However, the use of chemical control could potentially be problematic for two reasons, firstly because of non-target impact on underlying vegetation and secondly the typical proximity of invasions to waterways makes environmental contamination a threat (Simelane et al. 2011). Another key problem in the management of *Cardiospermum* invasions is the persistent seed bank. If the weedy canopy is cleared it opens the door for long-lived seeds to sprout (FloraBase 2012).

Management and problems in South Africa

In collaboration with South Africa's Working for Water program, a biological control programme was initiated against *C. grandiflorum* in 2003. However due to the taxonomic uncertainty surrounding *C. halicacabum* and *C. corindum* (discussed earlier, Table 1), biocontrol agents cannot be released, hampering effective management in South Africa. The importance of clarifying the geographic native ranges of all *Cardiospermum* species currently found in South Africa for the successful biological control of *C. grandiflorum* is therefore evident. If *C. corindum* and *C. halicacabum* are indeed native to southern Africa, only agents that are specific on *C. grandiflorum* can qualify for release in South Africa, and thus far, these agents have proved particularly difficult to rear and test under quarantine conditions (D. Simelane, pers. comm.). On the other hand, if *C. corindum* and *C. halicacabum* are not native to southern Africa, all suitable agents against *C. grandiflorum* qualify for release in South Africa.

Molecular systematics of *Cardiospermum* species in southern Africa

To determine the relationship between *Cardiospermum* species occurring in Africa and South America we sequenced two accessions of *C. grandiflorum*, *C. halicacabum* and *C. corindum* from each continent (South America and Africa). DNA was extracted from dried plant material using the CTAB method (Doyle and Doyle 1990). The internal transcribed spacer gene region was amplified using primers ITS1 and ITS4. A phylogenetic tree was then reconstructed in BEAST version 17.4 (Drummond et al. 2012) using a General Time-Reversible (GTR + G) model with uneven rates of evolution between base pairs.

The retrieved phylogeny indicates a close relationship between samples from South America and southern Africa (Fig. 3). For *C. grandiflorum* and *C. halicacabum* southern African samples are more closely related to South American samples than to other samples from southern Africa (i.e. geographic paraphyly). It is therefore likely that *C. halicacabum* in southern Africa, like *C. grandiflorum*, represents a recent introduction, and is therefore not native. For *C. corindum* however the phylogeny cannot dismiss natural long distance dispersal as an explanation for the species' presence in southern Africa, due to the southern African accessions forming a monophyletic group within the South American clade. The ability of *Cardiospermum* fruit to float in seawater for long periods of time and remain viable, makes a strong case for long distance dispersal. In order to clarify the uncertainty around human introduction versus rare long distance dispersal events, future phylogenetic analyses should include more and geographically widespread collections.

Bioclimatic preferences of *Cardiospermum halicacabum*, *C. grandiflorum* and *C. corindum*

Prevention is better than cure, with eradication of introduced species typically becoming less feasible as spread progresses (Thuiller et al. 2005). Identifying a species' suitable

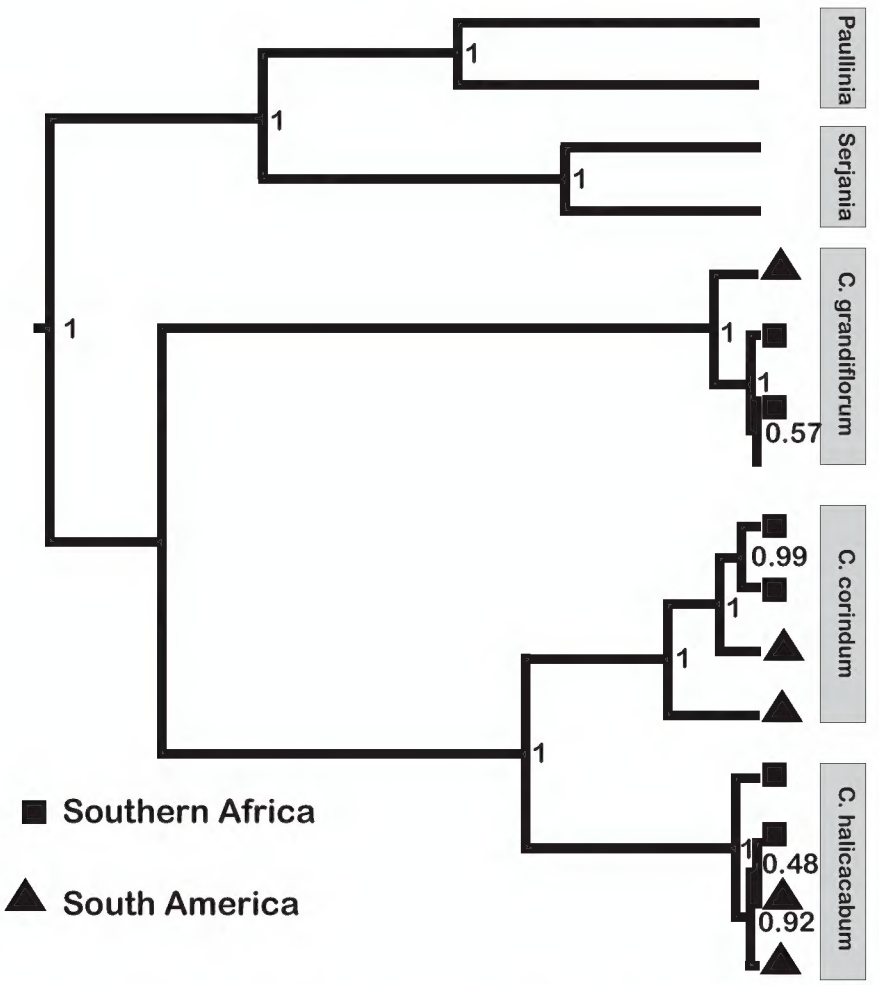

Figure 3. Cardiospermum phylogeny. Phylogeny of six South American and six southern African accessions of *Cardiospermum* species with *Paullinia* and *Serjania* species used as outgroup taxa. Topology support is shown as posterior probability at each node.

climatic range can therefore help to determine areas where introduction should be prevented or management intensified. Species distribution modelling is probably the most popular method for determining such areas (Allouche et al. 2006, Hirzel et al. 2006). Essential to the accuracy of species distribution modelling is the assumption that niche shifts do not occur in a newly introduced area, which has been shown to occur rarely (Petitpierre et al. 2012).

Modelling methods

We used BIOMOD version 1.1.5 (Thuiller et al. 2009) implemented in R version 2.15.1 (R Development Core Team 2012) to predict potentially suitable climate habitats for *C. halicacabum*, *C. grandiflorum* and *C. corindum*. Locality records were sourced from public databases [GBIF; Henderson 2007] and personal observations. We discarded records with spatial uncertainty (e.g., points in the ocean) and those from botanical gardens or with missing or duplicate values. Since no absence data is available for *Cardiospermum* species, but is needed for modelling, 10,000 pseudo-absence background points were created per species, by random sampling of the Köppen-Geiger climate classification. We employed generalized boosted regression models (GBM), a method uniting regression trees with boosting (for a more comprehensive

Table 2. Contribution (%) of each BioClim variable used for distribution modelling of *Cardiospermum* species. The first value in each species column is for global and the second for native range modelling.

Variables used for modelling	Variable importance					
	C. halicacabum		***C. grandiflorum***		***C. corindum***	
	Global	**Native**	**Global**	**Native**	**Global**	**Native**
Min temperature of the coldest month	21.2	12.5	13.8	25.4	14.9	21.1
Max temperature of the warmest month	6.2	2.3	4	0.9	3.9	1.7
Precipitation of the coldest quarter	4.9	22.2	27.8	25.9	13.7	2.1
Precipitation of the driest month	2	1.1	13.1	2.5	3.6	16.9
Precipitation of the warmest quarter	44.5	8.3	20	22.1	31.5	2.7
Temperature seasonality	17.2	57.6	22.8	24.9	6	7.9
Precipitation of the wettest quarter	-	-	3.2	5.7	34	42.5

description see Elith et al. 2008). For all analyses, seven climatic variables were sourced from BioClim (Hijmans et al. 2005), based on their importance for species survival and low co-linearity (Table 2). Importance, and thus the contribution of each variable to the model was assessed using Pearson rank correlation between standard predictions and those based on random permutations for each variable separately (Thuiller et al. 2009). If correlations between these two predictions were high, the specific variable was regarded as less important. Co-linearity between different variables was limited to <0.70 using Spearman rank correlation coefficients. Consequently, precipitation of the wettest quarter was dropped for modelling of *C. halicacabum* due to a high correlation with precipitation of the warmest quarter. A raster of 6 arc min was used to extract variables since a more coarse resolution is realistic for global scale prediction, while also accounting for sampling error. Models were calibrated with 70% of the data and evaluated with the remaining 30%. A cut-off value was determined with BIOMOD's default setting, representing the best probability threshold which maximizes the percentage of presence and absences correctly predicted for the evaluation data (Thuiller et al. 2009). Area under the receiver-operator-curve (AUC, Hanley and McNeil 1982) and the true skill statistic (TSS, Allouche et al. 2006) were used for model evaluation. AUC scores between 0.95 and 1 indicate an excellent, 0.9 and 0.95 a good and 0.6 and 0.8 a fair model (Thuiller et al. 2005). TSS values of 0.8–1 are excellent, 0.6–0.8 good and 0.0–0.6 fair for predicting accuracy (Allouche et al. 2006).

The accuracy of species distribution modelling is influenced by false positives and negatives (Thuiller et al. 2005, Fawcett 2006). Therefore a second aim of our species distribution modelling approach was to evaluate the accuracy with which this technique can predict potential invasive regions using models calibrated with native range data only. South and Central America were used as the native range for all three species since native status is debated in all other regions. A model calibrated using these records were then used to project suitable climate regions globally as described above. Known global occurrence records were then used as independent data to evaluate modelling accuracy.

Modelling results

Australia: Global data models for all three species performed well, with AUC values above 0.9 and TSS values above 0.65 (Table 3). Bioclimatic predictions show that a large proportion of Australia is climatically suitable for *Cardiospermum corindum*, a species currently absent in this country. Both *C. halicacabum* and *C. grandiflorum* have been introduced to Australia and are classified as invasive weeds. The suitable climate range for *C. corindum* in Australia is much larger than predicted for both *C. grandiflorum* and *C. halicacabum* and as such ornamental or medicinal introductions of *C. corindum* into Australia should be prevented (Fig. 4A, B, C). Modelling also predicted that the east coast of Australia is climatically highly suitable for *C. halicacabum,* such that any risks from its establishment in this area should be assessed. *Cardiospermum grandiflorum* appears to be a more rapid colonizer than *C. halicacabum* in Australia and it is already present in most predicted areas. It is however likely to become locally more abundant in areas where it is already found (Fig. 1B and Fig. 4B).

Europe and Asia: Our modelling approach identified Europe as mostly climatically unsuitable for *Cardiospermum* (Fig. 4A, B, C). Areas of suitable climate are present for all three species in certain parts of Asia including India (where *C. halicacabum* and *C. corindum* are present), Thailand and Pakistan, with *C. grandiflorum* potentially being the most restricted taxon (Fig. 4B). *Cardiospermum corindum* has high climatic suitability in southern Yemen, southern India, Thailand, Myanmar and southern China (Fig. 4A). The southernmost tip of Yemen seems climatically suitable for *C. halicacabum*, with India, Thailand, Cambodia, Vietnam, Myanmar, Japan, Taiwan and parts of China highly suitable (Fig. 4C). Many of these regions are already occupied by *C. halicacabum*. Climatically suitable habitat for *Cardiospermum grandiflorum* in Asia only appears to be present in southern India, Sri Lanka and parts of Vietnam (Fig. 4B).

Southern Africa*:* In South Africa bioclimatically suitable areas for *C. grandiflorum* are in the Western Cape Province, while for *C. halicacabum* they are in coastal areas in the Eastern Cape Province. Bioclimatically suitable areas in South Africa are the largest for *C. corindum,* with the Western and Eastern Cape Provinces being highly suitable. Currently the species is limited to Limpopo, Mpumalanga and northern parts of Kwazulu Natal (SANBI). Spread and anthropogenic movements of *Cardiospermum* species

Table 3. Evaluation of modelling predictions. True skill statistic (TSS) and area under the receiver operating characteristic (ROC curve) (AUC) for global and native range modelling of three widespread *Cardiospermum* species. The first value in TSS and AUC column is for global and the second for native range modelling. Independent data evaluation is for the native range models evaluated against known non-native ranges.

Species	TSS		Independent data (TSS)	AUC		Independent data (AUC)
	Global	Native	Native	Global	Native	Native
C. halicacabum	0.651	0.703	0.441	0.9	0.923	0.755
C. grandiflorum	0.759	0.665	0.343	0.95	0.895	0.639
C. corindum	0.689	0.629	0.565	0.905	0.896	0.881

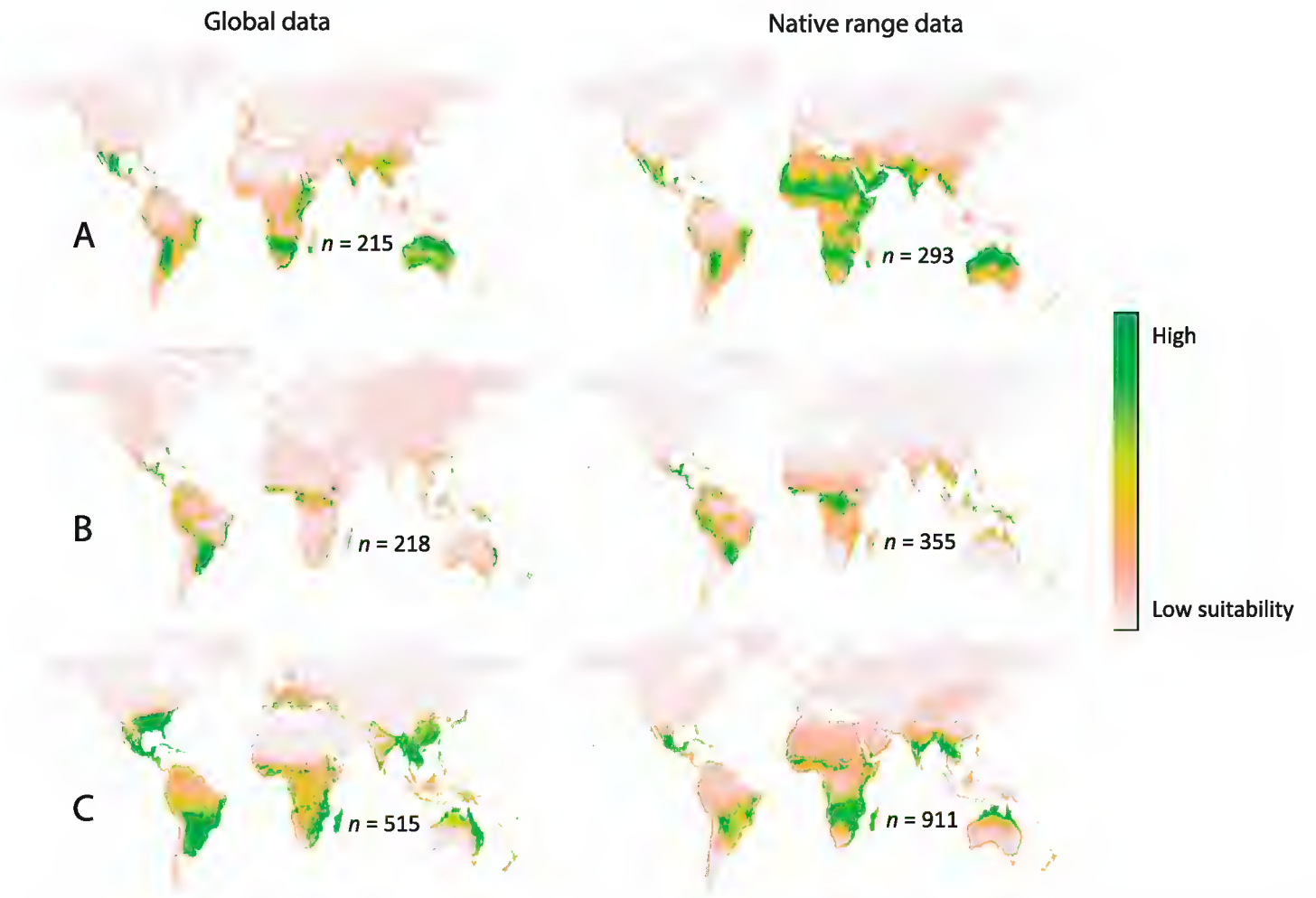

Figure 4. Species distribution modelling of *Cardiospermum* species. Global climatically suitable ranges for **A** *C. corindum* **B** *C. grandiflorum*, and **C** *C. halicacabum* as predicted by boosted regression trees in BIOMOD using global (left) and native range data (right). Number of occurrence points used for modelling (*n*) is indicated on each map.

in South Africa should therefore be closely monitored since a large part of South Africa appears climatically suitable for establishment. While *Cardiospermum grandiflorum* and *C. halicacabum* are recorded as naturalised in parts of Namibia and Botswana, bioclimatic modelling did not predict either country as climatically suitable. *Cardiospermum* species are not widespread in these two countries and possibly only occur in areas with suitable microclimates. Such habitats typically differ significantly from surrounding environments and often result from human actions, and are therefore excluded in bioclimatic modelling based on more coarse data, such as this study (Kearney and Porter 2009).

Testing model accuracy

Models calibrated with South and Central American native occurrence records performed fairly well when cross-validated using AUC and TSS, with values higher than 0.85 and 0.6 respectively. However this was not the case when these models were evaluated with independent data, thus known presence data not used in modelling. *Cardiospermum halicacabum* and *C. grandiflorum* had low AUC and TSS values ranging between 0.60–0.80 and 0.30–0.45 respectively, only *C. corindum* models performed fairly well (AUC > 0.85 and TSS > 0.55, Table 3).

These results indicate that models calibrated with native range occurrence records only, would not have accurately predicted the invasive spread of *C. grandiflorum* in South Africa while underestimating its potential range in Australia. This lack of accuracy for identifying invasive regions using native data questions the suitability of using species distribution modelling alone when determining potential invasive regions.

Also contrary to what we expected, models calibrated using native range data predicted larger climatically suitable areas than models calibrated with global range data (Fig. 4; except for *C. halicacabum*). We hypothesised that this is due to the more restricted climate zones created with the widespread pseudo-absence data of the global range, thus including more diverse habitats to exclude as suitable areas. We plotted the presence and absence points for both native and global range data for each variable against the probability of occurrence using the response plot function in R (Appendix, Fig. S1 A–F). In these figures it is clear that global data variables include a wider environmental range for pseudo-absences compared to the native range pseudo-absences, especially when considering the most significant variables based on variable importance (Table 2). To test if this is indeed the case we ran three additional models with the same settings as the previous models but using native range presence data and global pseudo-absences data. We used the same evaluation parameters as for the previous models (Appendix, Table S1, S2). This approach resulted in projections that more closely resembled global range model predictions or are even more restricted predictions (Appendix, Fig. S2). These results indicate that while native range data can be used to predict potential suitable areas, data are often over-fitted, thus over predict the extent of suitable habitats, due to less restricted absence data created from the native range.

Usefulness of bioclimatic species modelling

While species distribution modelling is a popular tool for predicting potential invasive ranges its accuracy remains questionable (Araújo and Luoto 2007, Sinclair et al. 2010). Bioclimatic modelling did not accurately predict current invasive regions for the widely naturalized species *C. grandiflorum*. Also native range data alone led to an over estimation of potential suitable habitats for *C. corindum* and *C. grandiflorum*. Our results comparing predictions based on native and global occurrence records are surprising and significant. We hypothesized that the reason for this observation is the more restricted climate zones created when using global pseudo-absences for model calibrations, an effect that can potentially be amplified for species characterised by incomplete range filling in their native ranges. A key assumption of species distribution modelling is pseudo-equilibrium, however this is probably unrealistic for most species and may therefore seriously impact model accuracy (Guisan and Thuiller 2005). On the other hand, bioclimatic predictions may be hampered if a species has undergone a niche shift in its invasive range (Broennimann et al. 2007). All the above-mentioned issues highlight how factors other than climate may play a crucial role in the accuracy of species distributions modelling. For example niche shift in the non-native range could be the result of release from natural enemies

(Keane and Crawley 2002). Similarly, increased resource availability in the introduced range (Davis et al. 2000, Thompson et al. 2004) may increase habitat suitability while abiotic attributes of the new range may permit spread into novel habitats. In concert, dispersal limitations (Pulliam 2000), anthropogenic effects and unique historical factors (Jiménez-Valverde et al. 2008) may limit the distribution of species in their native ranges.

Thus, taking the contradicting results into account and also considering the many other factors that influences a species distributional range, lead us to conclude that while bioclimatic modelling is a useful approach, it should not be used as a stand-alone tool when making conservation decisions regarding the introduction of species into a novel range and caution should be exercised to ensure the quality of input data while also taking other factors into account as discussed above.

Conclusions

Many regions globally appear climatically suitable for establishment of *Cardiospermum grandiflorum*, *C. corindum* and *C. halicacabum,* cautioning against further introductions. Resolving the native ranges for these species globally is therefore important for biodiversity conservation and invasive species management. For example, our preliminary results indicate that *C. halicacabum* from southern Africa have a close relationship with South American samples, but that rare long distance dispersal cannot be ruled out as an explanation, while the split between South American and southern African *C. corindum* hints towards a native status on both continents. Future work should include a more comprehensive phylogeny to substantiate our findings, including balloon vine specimens from other biogeographic regions where the native status is known. If it is found that they are indeed alien to Africa and Asia, a risk assessment challenge lies ahead since large areas of these continents appear climatically suitable for their establishment. No *Cardiospermum* species are regarded as native in Australia, and measures to limit the spread of *C. halicacabum* and *C. grandiflorum* may be augmented with biological control measures that include native soapberry bugs that are evolving to use them more efficiently (Carroll et al. 2005b). In addition, the introduction of *C. corindum* should be prohibited based on the wide environmental suitability identified for this species in Australia.

Cardiospermum species are also used by many people in rural areas for medicinal purposes, further emphasizing a need to resolve the natal biogeographic distribution of this globally important genus to ensure its effective management, control or conservation.

Acknowledgments

We thank Dr Ingolf Kühn and the two anonymous reviewers for their constructive comments on previous drafts of the manuscript. Financial support was provided by the DST-NRF Centre of Excellence for Invasion Biology and the Working for Water Programme through their collaborative project on "Research for Integrated Management of Invasive

Alien Species". E Gildenhuys acknowledges the South African National Research Foundation's (NRF) Scarce Skills scholarship programme. J Le Roux also acknowledges Stellenbosch University's Sub-committee B "Young Researchers Fund" and the NRF Thuthuka Programme for research funding. S Carroll acknowledges support from the School of Life Sciences at the University of Queensland, St. Lucia. We are grateful to Jason Donaldson and Vernon Visser for their help and advice with species distribution modelling.

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Appendix

Supporting information for species distribution modelling of *Cardiospermum* species using native range presences and global pseudo absences. (doi: 10.3897/neobiota.19.5279.app) File format: Micrisoft Word Document (doc).

Explanation note: The file contains the response plots for variables used in species distribution modelling. Modelling predictions and the importance of individual variables in those models using native range presence and global absence data are also given.

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Citation: Gildenhuys E, Ellis AG, Carroll SP, Le Roux JJ (2013) The ecology, biogeography, history and future of two globally important weeds: *Cardiospermum halicacabum* Linn. and *C. grandiflorum* Sw. NeoBiota 19: 45–65. doi: 10.3897/neobiota.19.5279 The ecology, biogeography, history and future of two globally important weeds: *Cardiospermum halicacabum* Linn. and *C. grandiflorum* Sw. NeoBiota 19: 45–65. doi: 10.3897/neobiota.19.5279.app